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Target detection, shape discrimination, and signal characteristics of an echolocating false killer whale (*Pseudorca crassidens*)

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INTRODUCTION

False killer whales (*Pseudorca crassidens*) are pelagic, social, presumably deep-diving odontocetes that inhabit the temperate and tropical waters of the world's oceans (Leatherwood *et al.*, 1982). This species has recently been added to the list of small odontocetes known to echolocate (Thomas *et al.*, 1988b). A small body of information regarding its bioacoustic capabilities is available, which includes an underwater audiogram (Thomas *et al.*, 1988a), masked hearing levels (Thomas *et al.*, 1990), a range threshold for target detection (Thomas and Turl, 1990), and subsequent comparisons of *Pseudorca's* echolocation signal characteristics as recorded in concrete pools and open water. No echolocating capability other than detection has been demonstrated.

The only audiogram documented for *Pseudorca* (Thomas *et al.*, 1988a) is a typically mammalian U-shaped, broadband curve. The maximum sensitivity of 40 to 50 dB *re*: 1 μPa occurs between 16 to 64 kHz and corresponds to the peak frequencies of the echolocation signals of *Pseudorca* recorded in a concrete pool (Thomas *et al.*, 1988b). Like other small odontocetes that have been investigated, the critical ratios for *Pseudorca*, which ranged from 17 to 42 dB, are lower than those known for other mammals (Thomas *et al.*, 1990).

The initial demonstration of *Pseudorca's* echolocation ability (Thomas *et al.*, 1988b) was conducted in a concrete pool and showed that the animal could successfully detect a 7.62-cm-diam, water-filled, stainless steel sphere at a distance of 4 m. A later study conducted in open water with an identical target reported a detection range threshold of 117 m (Thomas and Turl, 1990). The peak frequencies (105–110 kHz) and -3-dB bandwidths (20–25 kHz) of the echolocation signals recorded in open water during that study were higher and broader than those emitted by a free-swimming whale and recorded in a concrete pool (20–65 kHz and 5–16 kHz, respectively).

The echolocation detection and discrimination capabilities of the Atlantic bottlenose dolphin (*Tursiops truncatus*) are impressive and have been well documented (cf. Nachtigall, 1980). Au and Snyder (1980) reported a maximum range of 113 m for a dolphin echolocating on a 7.62-cm, water-filled, stainless steel sphere. Nachtigall *et al.* (1980) investigated a dolphin's ability to discriminate between cylinders and cubes of varying sizes. Their probe-trial technique, in which target orientations were altered, revealed a dependence on target aspects; amplitudes of pulsed echoes varying relative to flat surfaces and remaining uniform relative to curved surfaces.

It has become evident that small odontocetes control the parameters of their emitted echolocation signals in response to any of several variables (Moore and Pawloski, 1991; Au,

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1980; Evans, 1973; Norris *et al.*, 1972; Turner and Norris, 1966). Au (1980) and Au *et al.* (1985) reported that source level (SL) and peak frequency in the signals emitted by the Atlantic bottlenose dolphin (*Tursiops truncatus*) and the beluga whale (*Delphinapterus leucas*) varied as a function of the level of ambient noise. Moore and Pawloski (1991) reported voluntary control over SL and peak frequency in the echolocation signals of *Tursiops*. They suggested that changes in echolocation signal parameters may depend on the task being performed and noted that as the animal increases source level, the peak frequency of the emitted signal shifts from low to high. Contrary to their expectations, Brill and Harder (1991) did not observe an increase in the SL's of a dolphin's (*Tursiops truncatus*) emitted signals when the returning echoes were experimentally attenuated at its lower jaw. They assumed that their dolphin did not increase SL due to limitations imposed by the physical nature of a concrete pool on the range of useful energy in the emitted clicks. Thomas and Turl (1990) suggested that the differences in reverberation and background noise in a concrete pool as opposed to open water was responsible for the difference in peak frequencies and bandwidths observed in their studies of *Pseudorca's* emitted echolocation signals. In either of those environments, the false killer whale's performance during target detection by echolocation, albeit in a lower frequency range, is remarkably similar to that reported for *Tursiops truncatus* (cf. Au, 1990).

The goals of this study were to further investigate the echolocating capabilities of *Pseudorca* by demonstrating the subject's ability to discriminate between two targets, and to examine parameters of the subject's outgoing signals for any changes that may be related to target range, task, or learning. The training and conduct of this study included three phases; target detection, target range extension, and target discrimination. Since previous observations of *Tursiops*' echolocation emission parameters showed shifts in frequency and source level, which were interpreted as changes in response to either task or ambient noise, we monitored this *Pseudorca* for changes in emitted signals when target range increased or when the task changed from detection to discrimination. Since the transmission losses increased by 36 dB as target range increased from 1 to 8 m, we hypothesized that there would be an increase in the source level of the whale's emitted signals. Also, if there was a marked difference in task difficulty between detection and discrimination, we expected that difference might result in changes in emitted signals.

I. METHODS

A. Subject

The subject was a 6-yr-old, female false killer whale who was previously trained for a masked hearing study (Thomas *et al.*, 1990) but had no previous conditioning for echolocation tasks. The whale's age, previous performance in the masked hearing study, and her detailed medical history suggested that her hearing capabilities were normal.

B. Equipment and procedure

Our experiment was conducted in 9-m × 12-m section of a floating pen complex (Fig. 1) in Kaneohe Bay, Oahu, Hawaii. Echolocation detection and discrimination tasks were conducted using a "go/no-go" paradigm (see Schusterman, 1980) in the physical configuration shown in Fig. 1. A trial began with the whale stationed facing the trainer in the instrumentation shelter. At the onset of a 7-kHz underwater tone, the whale left her station to position herself in an underwater, stainless steel hoop centered 1 m below the water's surface. An underwater video camera mounted to the right of the hoop made it possible for the trainer to verify the whale's position. Once properly positioned, a screen used to block the whale's visual and acoustic access to the target was lowered allowing the whale to ensonify the target for three seconds.

A machined aluminum cylinder, 12.7 cm × 3.785-cm o.d. × 3.15-cm i.d. (0.64-cm wall thickness), was used as the standard or "go" target in all phases of this study. If the whale detected the "go" target, she backed out of the hoop immediately to depress a response paddle. If a "no-go" condition was detected (the absence of the "go" target or the presence of any other target), the whale would remain in the hoop station for 10 seconds after the screen was raised to its starting position. The whale would then leave the hoop at the sound of a bridging cue, a whistle sounded by the trainer, to return to the trainer and reposition for the next trial. All correct responses were reinforced with a fish reward.

The number of trials per session varied across conditions as described below. The order of target presentation was determined by Gellerman tables (Gellerman, 1933) modified to set the 1st order conditional probability of a "go" following a "no-go," or vice versa, at 0.50 over each block of 10 trials in a 100-trial series.

C. Target detection and range extension

The whale was first conditioned to detect and report the presence or absence of the standard target. The target was

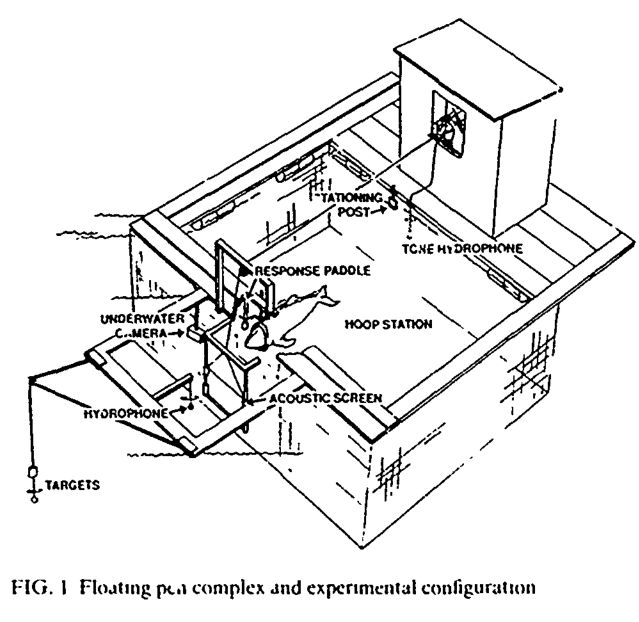

FIG. 1. Floating pen complex and experimental configuration.

initially placed 0.5 m in front of the hoop. A monitoring hydrophone was used during training to verify that the whale was echolocating and not relying on vision alone to accomplish the task. When the whale's performance was satisfactory (> 90% correct), the target range was increased in 0.5-m increments each time the whale's performance exceeded 80% until a range of 3 m was achieved. The number of trials per session were arbitrary during this training period.

At the 3-m range, the whale was tested in sessions of 25 trials each until the performance rate exceeded 90% in three consecutive sessions. Given the natural turbidity of the water and the fact that a human observer in the whale's hoop station could not visually detect the targets at the 3-m range, it was reasonable to assume that visual cues were completely eliminated at this range. The target range was then increased in 1-m increments each time the performance rate exceeded 90% in one 25 trial session until a distance of 8 m was achieved. The only exception was an abbreviated 10 trial session at the 7-m range.

D. Discrimination

Conditioning and testing for target discrimination was conducted at the 8-m range. During each trial either the standard cylinder ("go") or a 7.62-cm water-filled, stainless steel sphere ("no-go") was presented. Discrimination testing consisted of ten sessions of 50 trials each for a total of 500 trials.

The target strength of the sphere (− 28 dB) was lower than that of the standard cylinder (− 20 dB). To investigate whether or not the whale used target strength as a primary cue to discriminate the cylinder from the 7.72-cm sphere, we manipulated the target strength relationship by comparing the standard cylinder to a larger sphere (22.86-cm diameter) of greater target strength (− 14 dB) in one, 50-trial session. Finally, a 60-trial session was conducted during which both spheres were compared to the standard cylinder in counterbalanced blocks of 10 trials.

E. Recordings

We recorded samples of individual clicks emitted as the whale echolocated during target detection at ranges of 4, 5, 6, and 8 m and during target discrimination at the 8-m range. Emitted echolocation signals received by a Bruel & Kjaer 8103 hydrophone placed 2 m in front of and in line with the center of the hoop station were bandpassed through an Ithaco filter/amplifier set at 4.0 and 300 kHz. Signals were initially recorded on two channels of a Racal Store 4DS tape recorder operating at 60 in./s providing an effective bandwidth of 300 Hz–300 kHz. Later recordings were made on a Compaq Portable 3 computer using an RC Electronics computer scope (model ISC-16), which collected 256 points digitized at 1 MHz (12-bit resolution) for each click and stored the data on diskettes. Both recording methods were compared to each other for fidelity before analysis.

Signal analysis was performed on a personal computer to calculate the peak-to-peak source level and perform a fast Fourier transform (FFT) of each digitized click. Source level (SL) is defined as the sound pressure level of a click referenced to a distance of 1 m from the whale. The peak frequency and − 3-dB bandwidth were determined from the FFT results. Each click was analyzed individually and averages for each trial were computed.

II. RESULTS

A. Behavioral

The establishment of the "go/no-go" procedure and the detection task, beginning at a range of 0.5 m and extending to 3 m, was accomplished over a period of about 4 months. The number of trials and performance rates at each range between 3 and 8 m are shown in Table I. Once the whale's detection capability was established at the 3-m range (mean = 92% correct over 250 trails), a total of 160 trials was required to extend the range to 8 m. Detection performance varied between 88% and 100% correct for ranges between 3 and 8 m (mean = 93.45, s.d. = 6.74). Since the whale's performance at the 7-m range was obviously successful, it was decided to abbreviate that session and immediately extend the target range to 8 m. The whale's performance was not affected by that decision.

The whale's transition from the detection task to the discrimination task was made quickly and without any difficulty as evident in consistently high performance rates. The initial discrimination session, conducted after the whale had experienced a seven day break in testing, began with a warm-up of only five trials in the detection mode. Without interrupting the session, the 7.62-cm sphere was introduced into the procedure as the comparison target and the whale went on to score 80% correct in the discrimination mode over the

TABLE I. Values for target range and performance rates are given for sessions over which the whale's detection capability was established at 3 m and the target range was increased to 8 m. Session 15 was arbitrarily abbreviated in favor of moving to the 8-m range.

Session No.	No. of trials	Range (m)	% Correct
1	25	3	84
2	25	3	88
3	25	3	84
4	25	3	96
5	25	3	100
6	25	3	80
7	25	3	88
8	25	3	100
9	25	3	100
10	25	3	100
11	25	4	92
12	25	4	100
13	25	5	96
14	25	6	100
15	10	7	100
16	25	8	88
17	25	8	96
	410		mean = 93.45 s.d. = 6.74

remaining 50 trials. Performance over 500 discrimination trials varied between 80%–100% correct (mean = 91.8, s.d. = 5.76) as shown in Fig. 2. The whale's performance was similarly unaffected (90% correct) during a 50-trial session in which the smaller sphere was replaced by a larger, 22.86-cm-diam sphere, reversing the target strength of the standard and comparison targets. Finally, performance rates consistently remained high when the standard target was compared to either the smaller (mean = 90, s.d. = 8.16) or larger (mean = 96.7, s.d. = 4.71) sphere in a 60-trial session as shown in Fig. 3.

B. Acoustic

A summary of the signal data recorded in this experiment is provided in Table II. A click and its FFT typical of the whales emitted signals are shown in Fig. 4. The mean peak frequency was 38 kHz, well within the range of peak frequencies reported for *Pseudorca* in a concrete pool. The mean peak-to-peak SL (*re*: 1 μPa) for detection was 175 dB. It was significantly higher than the mean peak-to-peak SL of 166 dB for discrimination [$t(234) = 14.56, p < 0.05$]. These SL's are just above those reported for *Pseudorca* in a concrete pool (Thomas *et al.*, 1988b) and clearly lower than those reported for open water (Thomas and Turl, 1990). The mean bandwidth was 45 kHz for detection and 35 kHz for discrimination, a significant difference between tasks [$t(260) = 6.37, p < 0.05$]. These bandwidths are broader than any previously reported for *Pseudorca* (Thomas and Turl, 1990).

During initial training for the detection task, the whale would occasionally emit high-frequency clicks (peak frequencies between 100 and 105 kHz). An example of such a click is shown in Fig. 5. These high-frequency clicks had frequency spectra similar to the high-intensity clicks (> 200 dB) measured by Thomas and Turl (1990), and were associated only for SL's that were above 185 dB. As training progressed, the whale gradually ceased to emit clicks above 185 dB with a corresponding disappearance of high-frequency clicks. The data seem consistent with the notion of Au *et al.* (1985), supported by Moore and Pawloski (1991), that high peak frequencies (> 100 kHz) are a by-product of producing high-intensity clicks.

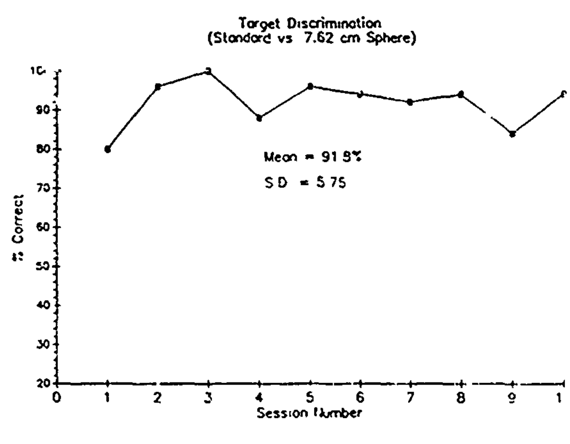

FIG. 2. Performance data for target discrimination (standard cylinder versus 7.62-cm sphere). Each data point equals 50 trials.

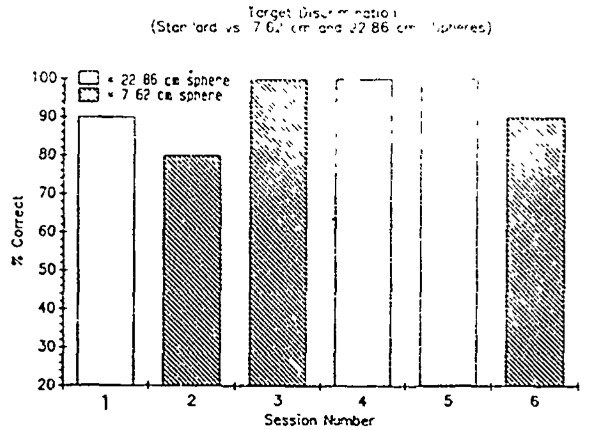

FIG. 3. Performance data for target discrimination (standard cylinder versus 7.62- and 22.86-cm spheres). Each session equals 10 trials.

Recognizing that cetacean echolocation clicks within a click train are not mutually independent events (Moore and Pawloski, 1991), multivariate analyses were used to investigate whether or not the whale had made any changes in the parameters of its outgoing signals as function of target range or task. Duncan's multiple range tests showed a significant decrease ($df = 185, p < 0.05$) in both SL and bandwidth in the transition from the detection to the discrimination mode at the 8-m range. Analysis of variance revealed a significant relationship between the number of clicks and test condition ($F(5,26) = 5.23, p < 0.0001$). Decreases in the number of clicks per trial were associated with the whale gaining experience in the detection task and the transition from the detection mode to the discrimination mode. There were no systematic changes in signal parameters (i.e., SL, peak frequency, bandwidth) as a function of target range. Occasional double clicks and bimodal frequency spectra (FFT) were observed. A sample waveform of a "double click" is presented in Fig. 6.

III. DISCUSSION

As would be predicted by the studies conducted by Thomas *et al.* (1988b) and Thomas and Turl (1990), the *Pseudorca* in this study performed well in target detection. After establishing the "go/no-go" procedure and recognition of the machined cylinder as the standard target during the initial four-month training phase, the whale progressed rapidly in the extension of target range. Likewise, the transition from the detection task to the discrimination task was easily accomplished and had no adverse effect on the whale's overall performance. The whale's ability to discriminate between two targets was clearly demonstrated.

Target strength is an obvious candidate for a decision-making criterion in this experiment. However, reversing the target strength relationship between the comparison and standard targets had no effect on our whale's ability to discriminate. Using a 166-dB signal, the *Pseudorca* would bare-

TABLE II. Summary of the parameters of signals recorded and analyzed during both detection and discrimination tasks.

Test condition	N trials	N clicks	Peak f (kHz) Mean	Peak f (kHz) s.d.	SL (dB) Mean	SL (dB) s.d.	BW (−3 dB) Mean	BW (−3 dB) s.d.
Detection:								
4 m	37	750	35.5	8.3	175.8	4.01	42.01	10.2
5 m	16	160	39.3	6.3	175.5	3.4	45.4	10.4
6 m	21	220	45.3	7.3	178.6	2.4	54.3	11.7
8 m	24	394	38.2	6.7	171.6	3.9	41.6	9.1
Discrimination:								
Small sphere	92	1214	36.7	16.4	168.5	5.6	37.7	12.9
Large sphere	72	1094	36.6	16.9	164.4	3.3	32.5	10.8

ly detect echoes from the 7.62-cm sphere but would easily detect echoes from the cylinder. While it is the most salient cue, we cannot be certain that target strength was the sole cue. Since the *Pseudorca* in our experiment maintained its performance level even after a reversal of the target strength relationship, it is possible that other cues in the returning echoes were useful for target discrimination.

The acoustic data collected in this study contribute further evidence for the plasticity and adaptability that small odontocetes demonstrate in emitting echolocation signals. Since the animal did not increase its overall emitted source level systematically as the target range increased, it seems apparent that the echo signal-to-noise ratio was sufficiently high for the task. This is not surprising in light of the target detection data provided by Thomas and Turl (1990) for an echolocating *Pseudorca* in Kaneohe Bay. They reported a performance rate of 90% for detecting a 7.62-cm sphere at a range of 95 m. The average peak-to-peak SL used by their whale was 221 dB *re*: 1 μPa. The difference in the two-way transmission loss for a target range of 95 m (with high-frequency clicks) and a target range of 8 m (with low-frequency clicks) is 51 dB. Therefore, in order for our whale's performance rate to be comparable to that reported by Thomas and Turl (1990), SL's of 170 dB for the 7.62-cm sphere, 162

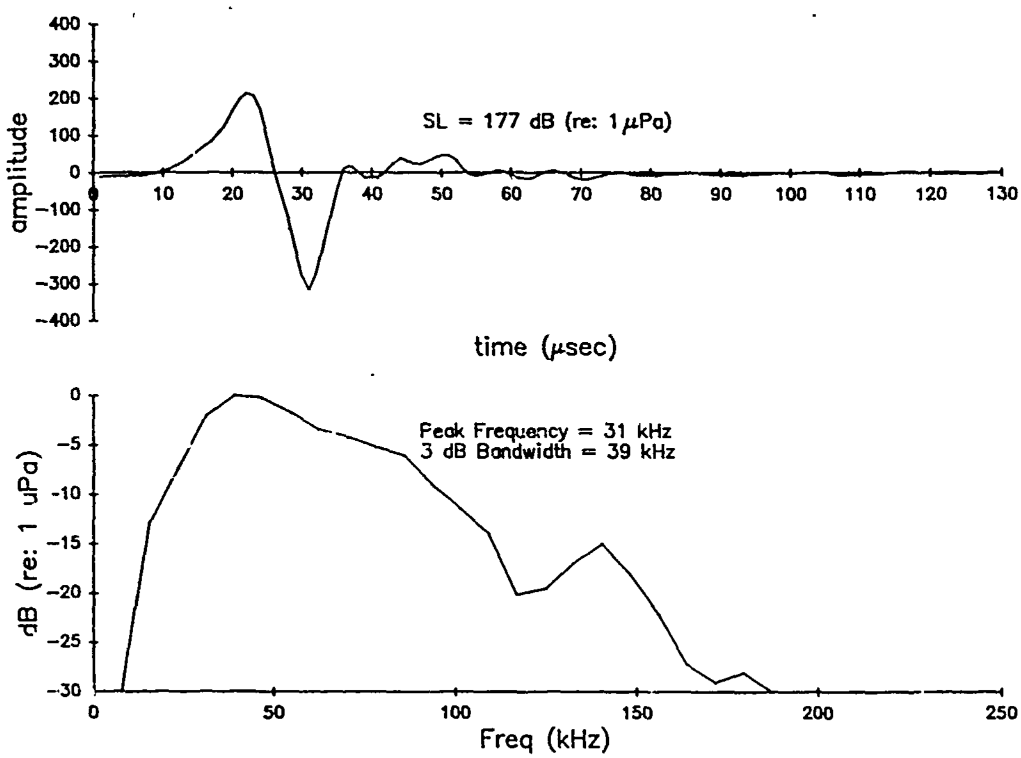

FIG. 4. The waveform and FFT of an echolocation click typical of those emitted by the *Pseudorca* in this experiment. Values for peak frequency, SL (*re* 1 μP, at 1 m), and −3-dB bandwidth are shown.

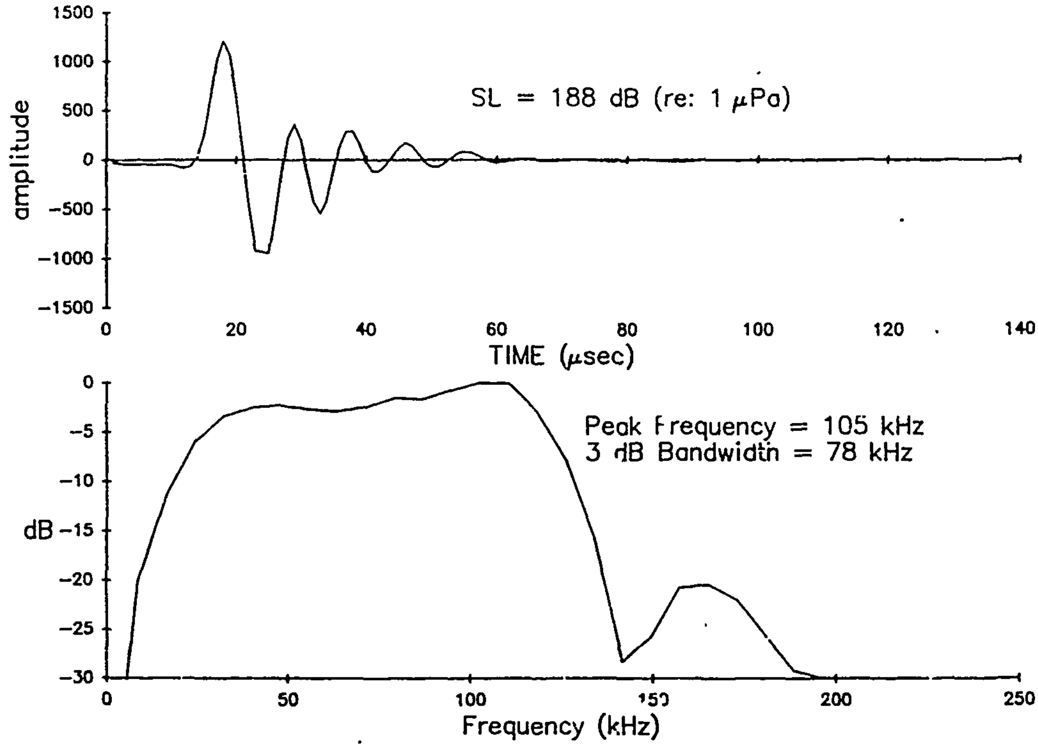

FIG. 5. Example of the high-amplitude/high-frequency clicks recorded during initial training stages for the detection task. These clicks had peak frequencies between 100 and 105 kHz and amplitudes greater than 185 dB.

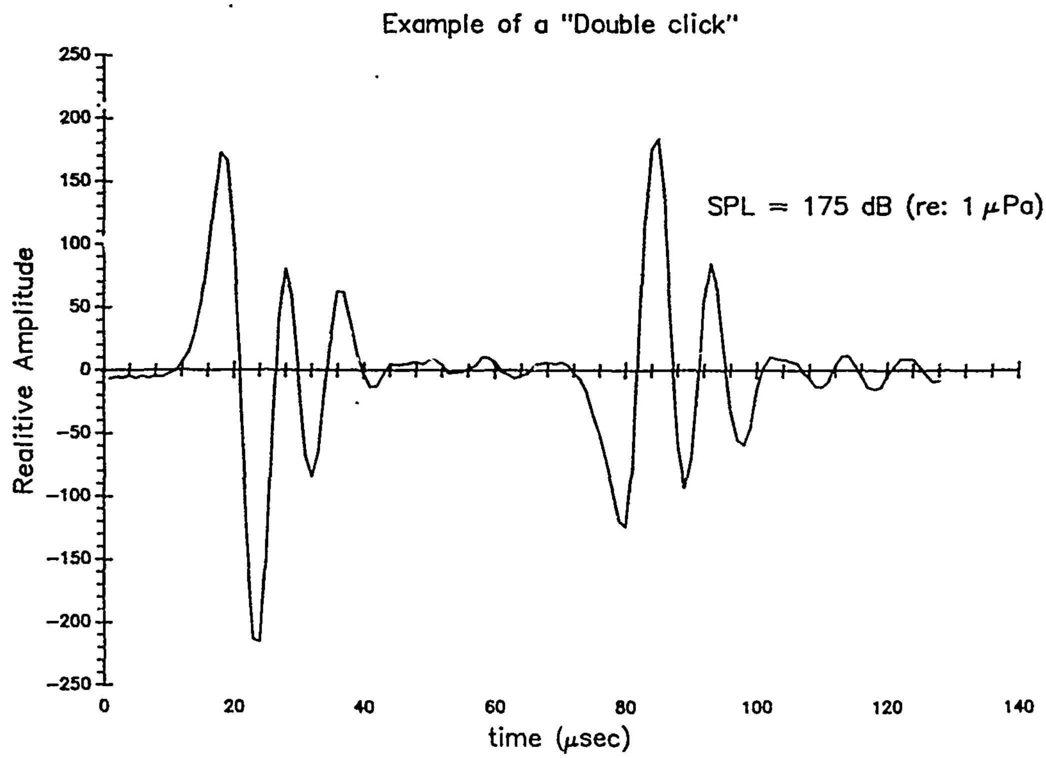

FIG. 6 Example of the few "double clicks" that were observed during the experiment The two waveforms are 180° out of phase and separated by 85 μs The second click is likely a reflection of the first off a pressure-release surface within the whale's head approximately 6 5 cm from the signal source

dB for the cylinder, and 156 dB for the 22.86-cm sphere would be required at a range of 8 m. These equivalent SL's are comparable to the 175 dB measured during the detection task and the 166 dB for the discrimination task (Table II).

There is also evidence that changes occurred as a function of task as observed in the changes in SL's and bandwidth associated with the transition from detection to discrimination. As the whale became more proficient at recognizing the standard target, she lowered her energy output by reducing the number of clicks, dropping the SL, and narrowing the bandwidth while maintaining high performance levels. Overall, the acoustic data support the hypothesis that small odontocetes control the parameters of their emitted echolocation signals as indicated by the changes in SL, bandwidth, and number of clicks per trial that we observed in the transition from the detection mode to the discrimination mode.

The "double click" shown in Fig. 6 is typical of the few that we observed during the experiment itself. Notice that the two waveforms are 180° out of phase and separated by 85 μs. It is likely that the second click is a reflection of the first off a pressure-release surface, perhaps an air sac, within the whale's head approximately 6.5 cm from the signal source. Double clicks were observed only for relatively low level signals. They were never observed when the SL's were greater than 175 dB. Thomas and Turl (1990) did not report any double clicks for their *Pseudorca*, which only emitted signals with SL's between 205 and 225 dB. We speculate that the double clicks emitted by this whale may be species specific artifacts of its signal generating mechanism related to low level signals rather than the result of any controlled manipulation of the emitted signal.

IV. SUMMARY AND CONCLUSIONS

This study provided the initial demonstration of a false killer whale's (*Pseudorca crassidens*) ability to successfully discriminate between two targets by means of echolocation. Performance indicates that *Pseudorca's* capabilities in the discrimination mode may be comparable to those of *Tursiops truncatus* (e.g., Nachtigall *et al.*, 1980). The whale's success in discriminating between a standard target and either of two different sized spheres suggest that other cues in addition to target strength were useful. The acoustic data recorded during initial target detection training, the extension of target range, and target discrimination, suggest that the whale had control over the parameters of its outgoing signals and that signal parameters changed as a function of task type and learning experience.

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